

XXI. *Parthenogenesis amongst the Workers of the Cape Honey-Bee: Mr. G. W. Onions' Experiments.* By RUPERT W. JACK, F.E.S., Govt. Entomologist, S. Rhodesia.

[Read October 7th, 1914.]

PLATES CV, CVI.

FOR some years past Mr. G. W. Onions, until recently a resident in the Cape Peninsula, has been engaged in following up a line of research, suggested by observations tending to show that the variety of the honey-bee mainly kept at the Cape exhibits a remarkable divergence from the European varieties, in that a far greater portion of the workers are apt to develop the habit of laying eggs, and that these eggs may produce either workers, queens or drones, but do, as a matter of fact, mainly produce workers.

As is well known, Dzierzon, Von Siebold and others held, and their views have been generally accepted, that the eggs of the "laying workers" and unfertilised queens of the honey-bee invariably produce drones, and founded on these and other observations we have the "Dzierzon theory" to the effect that the ova of the honey-bee are predominantly male whilst unfertilised, but that the female elements invariably predominate after the union of the ovum and spermatozoon. The production of a certain proportion of males by a fertilised queen was accounted for by supposing that the queen could control the egress of spermatozoa from the spermatheca when impelled by instinct to add a certain number of drones to the colony.

Of the merits or demerits of Dzierzon's explanation the writer is not qualified to judge, but the following paragraph is to be found on page 499 of the volume entitled "Peripatus, Myriapods, and Insects, Pt. I," by Sedgwick, Sinclair and Sharp, Cambridge Natural History: "The facts we have stated as to the sexes resulting from parthenogenetic reproduction in Hymenoptera generally, are extremely opposed to the Dzierzon theory, in so far as this relates to the production of sex. There have always been entomologists who have considered this view unsatisfactory."
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factory, and the observations of several recent French naturalists are unfavourable to the idea that the sex of an egg is determined by its fertilisation." Could it be shown, therefore, that in a variety of *Apis mellifica*, closely related to the variety with which Dzierzon and Von Siebold conducted their experiments, unfertilised eggs may and do produce female adults, the arguments of those opposed to Dzierzon's explanation would be very greatly strengthened, as few could credit the statement that the fact of the egg being fertilised or not determines its sex in respect to one variety of a species and not to all. An examination of Mr. Onions' claim to have proved the production of female offspring from Cape "laying workers," with a view to giving his remarkable discoveries wider publicity, is the object of this paper.

Concerning the actual variety with which Mr. Onions' experiments were conducted, Dr. Peringuey, Curator of the S.A. Museum at Cape Town, who kindly examined specimens for the writer, states that some authors consider the variety identical with the typical European *Apis mellifica*, L., but he himself is inclined to retain the varietal name *kaffra*, as given by Lepelletier. Specimens submitted to the British Museum were, however, judged to belong to the race *unicolor* var. *intermissa*, Latr. The identification of the exact variety, therefore, appears to be a somewhat difficult matter, and the writer is not in a position to express any opinion on the subject. The important fact is that this bee is very closely allied to the typical *Apis mellifica*, L.

As far back as November 1909 a notice appeared in the Agricultural Journal of the Cape of Good Hope stating that Mr. Onions had deposited with the Government Entomologist "an account of observations and experiments conducted by himself, which tend to show that laying workers of the native black honey-bee are far more common than is generally supposed, and that their eggs generally produce workers and not infrequently queens." A full account of these and other observations of a similar nature was published in the Agricultural Journal of the S.A. Union for May 1912. Since that time Mr. Onions has become a resident in S. Rhodesia, and has been able to repeat some of his experiments with bees imported from the Cape. Conditions in this territory are more favourable for such observations than those at the Cape, for the

reason that very few bees of the Cape variety are kept, whilst the native honey-bee of Rhodesia (*Apis mellifica unicolor* var. *adansoni*, B.R.) is easily distinguishable from that of the Cape. On account of this, any possibility of error through eggs having been stolen from other hives was entirely removed. It may be mentioned that although "laying workers" are, under certain circumstances, common enough in hives of the Rhodesian bee kept under domestication, their eggs have not been observed to produce anything but drones.

The account of Mr. Onions' observations, published as above, attracted but little attention, although a certain amount of adverse criticism appeared from the pens of one or two bee-keepers in the Union, and, anxious that his discoveries should be brought to the notice of scientists interested in parthenogenesis generally, the help of the Division of Entomology at Salisbury was sought, with the offer of experiments to be conducted under the supervision of an officer of the division.

Before proceeding to an account of these experiments it is desirable to call attention to one anatomical peculiarity in the Cape worker bee. In the typical *Apis mellifica* the spermatheca in the workers is, of course, vestigial, consisting merely of a slight projection from the common oviduct. This is also the case in the Rhodesian variety. In the Cape worker, however, the spermatheca is nearly spherical in shape, an average specimen measuring .54 mm. \times .45 mm. The writer has dissected upwards of sixty workers of this variety, and has found the spermatheca as above in every case. This observation is also due to Mr. Onions.

The development of the spermatheca naturally suggested the possibility of the Cape worker being adapted for fertilisation by a drone, possibly the diminutive form produced by fertile worker eggs—a condition of affairs which, though remarkable enough in itself, would have explained the production of female bees from worker eggs without subverting the fundamental nature of accepted principles in regard to parthenogenesis in bees. Careful examination, however, shows the laying workers to contain no spermatozoa, and the development of the sperm sac must apparently be regarded as merely in some way correlated to the reproductive potentialities of the insect, the organ itself being functionless.

The first experiment was commenced on December 24th, 1913, when Mr. Onions brought a bar-frame hive to the Experiment Station at Salisbury. This hive contained a strong nucleus of bees, one pure Cape and some crossed Rhodesian-Italian, introduced the day before, with seven frames of comb containing some honey and a very few eggs laid since the enclosure of the bees. All the comb was stated to have been taken from store and introduced into the hive the previous day. There was no queen present in the hive and no brood. The whole hive and colony was subjected to a searching inspection by the writer. On the 27th the hive was opened and thoroughly inspected again. More eggs had been deposited since the 24th, many being in the drone cells bordering certain of the frames. The writer again satisfied himself that no queen was present. The egg-laying appeared to be more systematic than is usually the case with the laying workers of European honey-bees, but more than one egg was frequently present in a cell, and on the whole the work might be described as intermediate between that of a normal queen and normal laying workers (see Plates CV, CVI). In two old queen cells a number of eggs were deposited.

On the 29th a considerable number of eggs had been laid in the two frames, and in one a number of young larvae were present, sometimes two in a cell. Some enlarged cells contained up to a dozen eggs, and the queen cells contained a great number which showed no sign of hatching. On January 3rd egg-laying was still confined to the two frames, and a number of the cells were now capped. Both old queen cells contained unhatched eggs.

Observations were continued until January 27th, by which time a number of young had emerged, all of which were of the black Cape variety and *workers*. Workers apparently emerged from the eggs laid in the *drone* cells, as no drones were present in the hive. On the 27th a frame of brood from the hive was taken into the laboratory and a number of workers were seen to emerge. All these were Cape bees. A few of the cells were now found to be capped in the well-known manner of worker cells destined to produce drones. These cells subsequently emitted small drones. The hive was next opened on February 5th, and the drone cappings were by this time more numerous, and a few small drones were present in the hive. Cape workers continued to emerge, however. This hive was

kept under observation until February 21st, in the hope that the bees would set up a queen cell, but although they hatched an egg in an old queen cell and fed the larva until nearly full grown, they subsequently allowed it to starve. In the meantime, another experiment was decided upon.

On February 21st, therefore, Mr. Onions installed a small colony of pure Rhodesian bees (var. *adansoni*) in a second hive, and in the writer's presence removed the queen. Two frames of honey only were carefully inspected and then placed in the hive, and two frames of Cape worker brood from the queenless hive used in the first experiment. The bees were brought in a swarm box, with the queen already caged. The two frames of honey were stated to have been in store for some time previously, and were certainly free from any eggs or brood at the time of insertion. The Rhodesian workers at once set up seven queen cells *on the introduced brood comb*, which were all sealed over by the 28th. On this day five of the queen cells were covered over with gauze cages, one was accidentally injured in manipulation, and one was left to hatch out normally. In the meantime, two other events had occurred. One of them was the appearance of mature Cape "laying workers," apart from young bees hatched from the introduced frame. These had evidently entered from the other hive, and Mr. Onions stated that in his apiary experience he had found that the Cape "laying workers" were accepted in almost any hive, and were, of course, an unmitigated nuisance on this account. The other event was the development of a number of Rhodesian "laying workers," which had scattered their eggs in great abundance through the drone cells on the two frames that had contained only honey. There were a dozen or more eggs in each drone cell, and an examination of several Rhodesian workers showed that they contained eggs in abundance.

The hive was not opened again until March 9th, when all the queens had hatched except two, which were dead in their cells. Two were alive in their cages and three dead outside. *All proved to be of the Cape variety.*

By this time it was impossible to deny that the Cape laying workers produced workers in abundance, and perfect females, if necessary. There was no possible source of error, because practically no Cape bees are kept in S. Rhodesia, and certainly there were none within miles of

the experimental hives, and yet in the queenless colony an abundant production of workers of the Cape variety continued, and only a small proportion of undersized drones appeared. Even had Cape bees been abundant near by it is impossible to imagine that some hundreds of eggs were stolen.

The question now remained as to whether these Cape workers could possibly have been fertilised. During the course of the experiment the writer had dissected a small number only of the Cape laying workers, examining the spermathecae under the microscope. The examination was checked by the dissection of a fertile and an unfertilised Rhodesian queen. The spermatheca was placed in saline solution on a slide and crushed under the cover glass. In the case of the fertilised queen, of course, myriads of spermatozoa were at once apparent. The spermathecae of the Cape workers, however, contained nothing but a jelly-like substance, which agreed on a smaller scale with the contents of the sperm sac in an unfertilised queen.

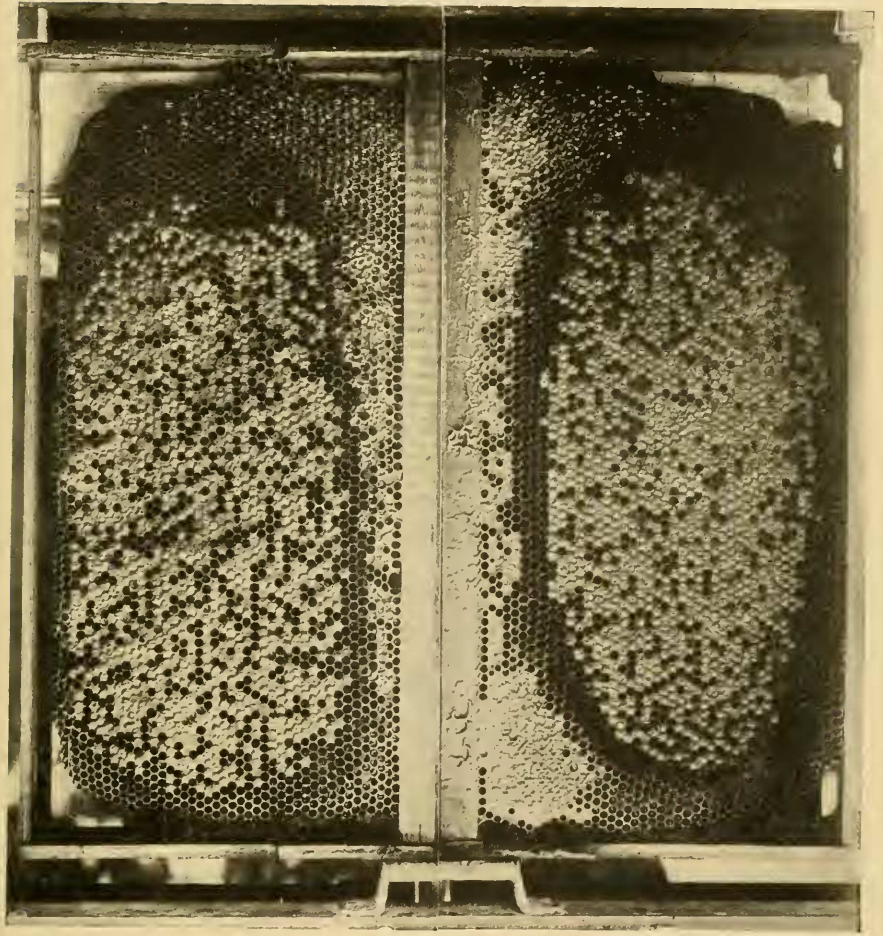
On request, Mr. Onions supplied a number of Cape workers from his apiary, which were found to contain eggs but no spermatozoa, but it was obvious that there was no certainty that these eggs were destined to produce workers, so that the dissections were of comparatively little value. A third experiment was therefore undertaken, and this served not only to prove that the Cape laying workers contained no spermatozoa, whilst producing worker bees, but also furnished a corroboration of both the other experiments.

On March 23rd Mr. Onions set up a new hive at the Experiment Station, giving its history as follows:—

On February 24th a hive of Rhodesian bees was “de-queened” and given a frame of Cape brood (from a queen). Two queen cells were matured—one of these was removed and one allowed to hatch. This hatched in due course, but on March 22nd the queen was found to be missing and Cape fertile workers strongly in evidence. The hive was examined by the writer and found to contain no queen. Three or four normal-sized Italian drones were present and many eggs, and some brood were present in the brood comb. These, of course, might possibly have been laid by the Cape queen, but this, as will be seen, did not affect the experiment in any way. A large number of black

Cape workers were present, and thirty of these were collected, and on dissection fourteen were found to contain eggs. There were no spermatozoa present. Other fertile workers were dissected on March 27th and on April 2nd with the same result. In the meantime, egg-laying continued and worker cappings appeared on the bulk of the brood in the combs, but about half a dozen drone cappings were in evidence amongst the worker brood. On opening, the latter were found to contain undersized drones. By April 2nd no drone cappings were present at all, and Cape workers were emerging freely. Five or six undersized drones were present amongst the bees.

Again, on April 8th nothing but worker cappings were seen, young bees were numerous and all of the Cape variety. Several were seen to emerge during the inspection. No drones at all were seen. On April 18th all the cappings were of the worker kind, Cape workers were emerging from the cells and numerous young Cape workers were present in the hive. The bees had constructed and sealed a queen cell in the meantime. One diminutive drone was seen. On the 27th the queen had emerged and was found in the hive. She had all the appearance of a pure Cape variety. Nothing but worker cappings were visible on the combs, and a long search was needed to find even one small Cape drone in the hive. By this date the queenless hive had been under the writer's observation for thirty-five days, during the last twenty-five of which no drone cappings had appeared and large numbers of Cape workers had emerged. This experiment, therefore, proved a clear corroboration of the first. The fortunate appearance of a queen served as a corroboration of the second experiment, whilst the fact that none of the fertile workers examined on March 23rd and 27th and on April 2nd contained spermatozoa, and that no drones emerged at any time that could possibly have been the progeny of eggs laid by these workers shortly before dissection (the period of development from egg to adult in the Cape variety agrees with that of European varieties), eliminated the exceedingly small possibility of an accident by which all the fertile workers taken for dissection might have been destined to produce drones. It is obvious that the eggs they were laying at the time they were caught produced workers only, and as no spermatozoa were present there can be no doubt that the eggs were parthenogenetically produced.



Photo, R. Jack.

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PARTHENOGENESIS IN CAPE HONEY-BEES.